

**LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
TRUPANEA ARIZONENSIS MALLOCH (DIPTERA: TEPHTRITIDAE) ON
TRIXIS CALIFORNICA KELLOGG VAR. *CALIFORNICA* (ASTERACEAE) IN
SOUTHERN CALIFORNIA**

RICHARD D. GOEDEN AND JEFFREY A. TEERINK

Department of Entomology, University of California, Riverside, CA 92521, U.S.A. (e-mail: rgoeden@ucr.ac1.ucr.edu)

Abstract.—*Trupanea arizonensis* Malloch is a monophagous, univoltine fruit fly (Diptera: Tephritidae) infesting flower heads of *Trixis californica* Kellogg var. *californica* (Asteraceae) in southern California. The egg, first- and third-instar larvae, and puparia are described and figured for the first time. As with each of the eight other *Trupanea* species previously studied, the lateral spiracular complex of the third instar is unique to *T. arizonensis*, comprising three verruciform sensilla on the meso- and metathorax and two verruciform sensilla on each abdominal segment. The third instar of *T. arizonensis* also differs from those of other *Trupanea* species previously studied in that both the meso- and metathorax are circumscribed by verruciform sensilla. The life cycle is of the aggregative type; whereby, the adults are long-lived and comprise the over-summering and over-wintering stage that returns with winter rainfall to aggregate on regrowing host plants for mating, and for oviposition during spring in the preblossom flower heads. The first instar tunneled into a single floral tube or ovule of a single immature floret, and each second and third instar continued its development by feeding principally on sap conducted to the excavated distal end of the same, then slightly stunted ovule. Pupariation occurs in the open flower heads, within which an average of 13% of the achenes were destroyed among heads containing puparia. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from individual puparia of *T. arizonensis* as a solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Trupanea*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, host-plant range, parasitoid

Trupanea arizonensis Malloch (Diptera: Tephritidae) is a rarely collected, monophagous or nearly monophagous species belonging to one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California (Foote and Blanc 1963, Foote et al. 1993). But, being of little or no economic importance, most species of *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until detailed life histories were published for nine

species from southern California (Cavender and Goeden 1982; Goeden 1987, 1988; Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of the immature stages of eight of these species (Cavender and Goeden 1982, Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991, Knio et al. 1996a, Teerink and Goeden 1998). This paper describes the life history and

most immature stages of a tenth species, *T. arizonensis*.

MATERIALS AND METHODS

This study was based in large part on dissections of subsamples of flower heads of *Trixis californica* Kellogg var. *californica* (Asteraceae) infested by *T. arizonensis* from samples collected during 1991–1995 in the low-elevation Colorado (northern Sonoran) Desert and high-elevation, eastern Mojave Desert in southern California in the manner described by Goeden (1985, 1992). The principal study sites in the Colorado Desert were Valliceto Valley at the mouth of Smugglers Canyon, 440-m elevation, San Diego Co.; the Edmund C. Jaeger Nature Preserve at 847 m, Desert Center, Riverside Co.; and Chino Canyon, 1 km NW of Palm Springs, at 270 m, Riverside Co. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Nine eggs, 18 first- and 16 third-instar larvae, and six puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL30-FEG scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton

wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Knio et al. (1996a), Goeden and Teerink (1997, 1998), Goeden et al. (1998a, b), and Teerink and Goeden (1998), and our earlier works cited therein. Means \pm SE are used throughout this paper. Voucher specimens of *T. arizonensis* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and now maintained by RDG.

RESULTS AND DISCUSSION

TAXONOMY

Adult.—*Trupanea arizonensis* was first described by Malloch (1942) as *Trypanea arizonensis*. Malloch (1942), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern, which Foote (1960) described as not sexually dimorphic, but essentially alike in every important character in the female and male. However, the variable nature of this wing pattern, especially among males, initially caused Goeden and Ricker (1989) to misidentify specimens reared from *Trixis californica* as *Trupanea actinobola* (Loew), another variable species (Foote and Blanc 1963, Foote et al. 1993, Goeden et al. 1998b). Goeden (1992) corrected this error and re-identified the flies from *T. californica* as *T. arizonensis*; moreover, Goeden et al. (1998b) further supported this identification based on the different tribal- and separate, subtribal-level, host-plant affiliations

of the three biotypes of *T. actinobola* in southern California, which exclude *Trixis californica* in the tribe Mutisieae (see below).

Nine (10.6%) of 85 ♂, but none of 65 ♀ of *Trupanea arizonensis* in the research collection of RDG reared from flower heads of *Trixis californica* have only one dark ray, not two rays, contrary to Foote et al. (1993), extending into cell dm from vein CuA₁. Moreover, the single, remaining, what is otherwise called the distal ray (Foote et al. 1993), is broken in cell dm and does not reach vein CuA₁ in 39 ♂ (45.9%) and 18 ♀ (27.7%). There is no dark spot on vein CuA₁ or on the wing margin in line with the broken distal ray in an additional 10 ♂ (11.8%) and 3 ♀ (4.6%), or with such a dark spot on CuA₁ or on the wing margin in line with the broken distal ray in an additional 2 ♂ (2.4%) and 3 ♀ (4.6%), respectively. The proximal ray usually extends, though sometimes very limitedly, into cell dm in 76 ♂ (89%) and all 65 ♀, and there is usually (not always, Foote et al. 1993) a dark spot on vein CuA₁ in line with it; however, in 3 ♀ (4.6%) the broken proximal ray is reduced to a spot in the middle of cell dm in line with a spot on vein CuA₁, and another 2 ♂ (2.3%) and 1 ♀ (1.5%) lack a dark spot in line with it. Therefore, all females and most males of *T. arizonensis* can still be distinguished from other *Trupanea* spp. by use of the separate keys for the two sexes in Foote et al. (1993) if one is aware of the above variations and perceives two dark rays, however abbreviated, extending into cell dm, neither of which necessarily crosses vein CuA₁, much less continues to the hind wing margin. Males with only one dark ray extending into cell dm from vein CuA₁, like the nine noted above, will run to *T. actinobola*, as they did earlier for Goeden and Ricker (1989). Couplet 8 (pp. 421 and 424 in Foote et al. 1993) distinguishing *T. maculigera* Foote from *T. arizonensis* apparently remains valid; although the angles formed by the proximal and distal rays, not the dis-

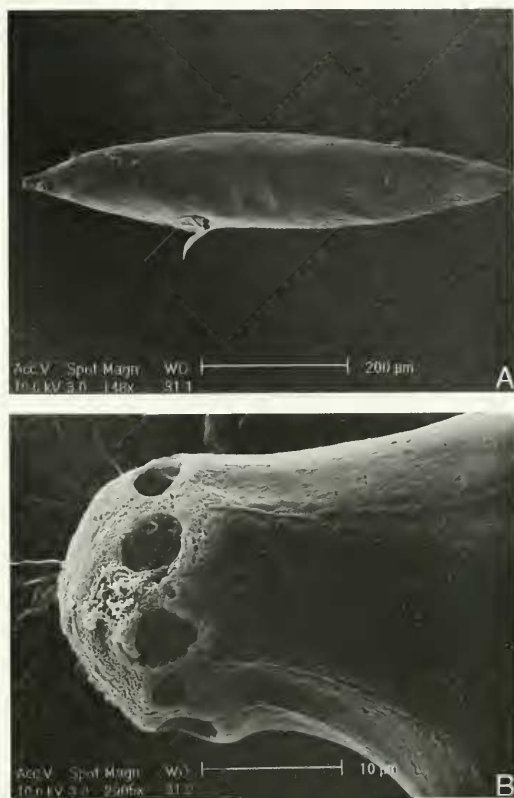


Fig. 1. Egg of *Trupanea arizonensis*: (A) habitus, pedicel to left; (B) pedicel.

tances between them along vein CuA₁, should be compared with specimens of *T. arizonensis* having proximal or distal rays or both broken in cell dm.

Immature stages.—The immature stages of *T. arizonensis* heretofore have neither been described nor illustrated.

Egg: Seventy eggs of *T. arizonensis* dissected from heads of *T. californica* were white, opaque, smooth; elongate-ellipsoidal, 0.70 ± 0.006 (range, 0.54–0.85) mm long, 0.15 ± 0.002 (range, 0.12–0.23) mm wide, smoothly rounded at tapered basal end (Fig. 1A), pedicel 0.02 mm long, with single row of subcircular aeropyles (Fig. 1B).

The egg of *T. arizonensis* is narrow like the eggs of *T. actinobola* (Goeden et al. 1998b) and *T. pseudovicina* (Goeden and Teerink 1998), but is much longer than both of these species. The egg body in *T. ari-*

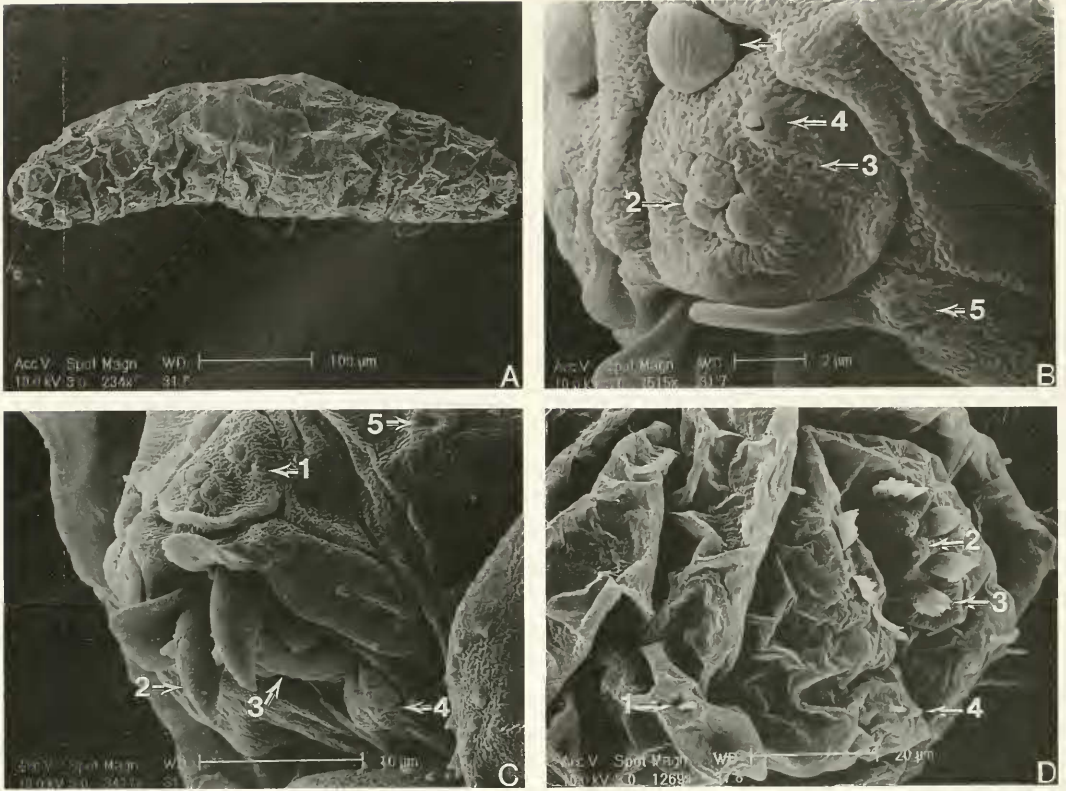


Fig. 2. First instar of *Trupanea arizonensis*: (A) habitus, anterior end to left; (B) gnathocephalon, anterior view, 1, dorsal sensory organ, 2, terminal sensory organ, 3, pit sensory organ, 4, lateral sensory organ, 5, stomal sense organ; (C) gnathocephalon, ventral view, 1, anterior sensory lobe, 2, mouth hook, 3, median oral lobe, 4, labial lobe, 5, pit sensillum; (D) caudal segment, 1, stelex sensillum, 2, rima, 3, interspiracular process, 4, intermediate sensory complex.

zonensis tapers smoothly into the pedicel, more so than in the other *Trupanea* species previously studied (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998). The pedicel is similar to these other congeners in having a single row of aeropyles (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Teerink and Goeden 1998), with the exception of *T. bisetosus* (Coquillett), which has one or two rows (Knio et al. 1996a).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines (Fig. 2A); gnathocephalon smooth (roughness in Fig. 2 is an artifact), lacking rugose pads (Fig. 2C); dorsal sen-

sory organ a dome-shaped papilla (Fig. 2B-1); anterior sensory lobe (Fig. 2C-1) bears terminal sensory organ (Fig. 2B-2), pit sensory organ (Fig. 2B-3), lateral sensory organ (Fig. 2B-4), and supralateral sensory organ; stomal sense organ indistinct (Fig. 2B-5); mouth hooks bidentate (Fig. 2C-2); median oral lobe laterally flattened (Fig. 2C-3), labial lobe (Fig. 2C-4) attached to median oral lobe; pit sensillum laterad of anterior sensory lobe (Fig. 2C-5); prothorax lacking rugose pads, few minute acanthae ventrad of mouth lumen; stelex sensilla circumscribe caudal segment in 2-dorsal, 4-ventral arrangement (Fig. 2D-1); posterior spiracular plates bear two ovoid rimae (Fig. 2D-2), and four, spatulate interspiracular processes (Fig. 2D-3); intermediate sensory

complex consists of a medusoid and stelex sensillum (Fig. 2D-4).

The first instar of *T. arizonensis* is very similar to other congeners previously studied in habitus and sensory structures (Goeden and Teerink 1998; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998). The lateral spiracular complex was not seen. There are slight differences in the interspiracular processes. In *T. jonesi*, the interspiracular processes are greatly reduced (Goeden et al. 1998a), in *T. arizonensis* and *T. conjuncta* the processes are single and spatulate (Teerink and Goeden 1998), and in *T. pseudovicina* Hering, *T. actinobola*, *T. bisetosa* and *T. nigricornis* (Coquillett), the interspiracular processes are divided, each with 1–4 branches (Goeden and Teerink 1997; Goeden et al. 1998b; Knio et al. 1996a).

Third instar: White, elongate-cylindrical, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines in bands increasing in width posteriorly (Fig. 3A); gnathocephalon conical, rugose pads dorsal and lateral to mouth lumen (Fig. 3B-1); dorsal sensory organ a dome-shaped papilla (Fig. 3B-2, 3C-1); anterior sensory lobe (Fig. 3B-3) bears the terminal sensory organ (Fig. 3C-2), pit sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5); stomal sense organ ventrolateral of anterior sensory lobe (Fig. 3B-4, 3C-6); mouth hooks tridentate (Fig. 3B-5, 3D-1); median oral lobe tapered anteriorly (Fig. 3D-2); six pit sensilla circumscribe gnathocephalon posterior to rugose pads (Fig. 3B-6); minute acanthae circumscribe anterior margin of prothorax (Fig. 3E-1); rugose pads (Fig. 3E-2) and a single row of verruciform sensilla (Fig. 3E-3) circumscribe prothorax posteriorad of minute acanthae; additional verruciform sensilla on dorsal half of prothorax (Fig. 3E-4); anterior thoracic spiracle on posterior margin of prothorax bears three ovoid papillae (Fig. 3E-5), meso- and metathorax circumscribed by verruciform sensilla; meso- and meta-

thoracic lateral spiracular complexes consist of a spiracle (Fig. 3F-1), and three verruciform sensilla (Fig. 3F-2); abdominal lateral spiracular complex consists of a spiracle (Fig. 3G-1) and two verruciform sensilla (Fig. 3G-2); caudal segment circumscribed by minute acanthae (Fig. 3H-1); posterior spiracular plates bear three ovoid rimae, ca. 0.03 mm in length (Fig. 3H-2), and four interspiracular processes, each with 3–5 branches, longest measuring 0.02 mm (Fig. 3H-3); intermediate sensory complex consists of a stelex sensillum and a medusoid sensillum (not shown).

The third instar of *T. arizonensis* is similar in general habitus to *T. pseudovicina* in being elongate-cylindrical, maybe even more attenuated (Goeden and Teerink 1998). As with the third instars of each of the eight other *Trupanea* species previously studied, the lateral spiracular complex is unique to *T. arizonensis*, with three verruciform sensilla in the meso- and metathorax and two verruciform sensilla in the abdominal segments (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998). There are other differences between individual species. *Trupanea arizonensis* differs from *T. actinobola* in lacking elongated integumental petals; *T. arizonensis* has fewer rugose pads circumscribing the prothorax, and the prothorax is completely circumscribed by minute acanthae (Goeden et al. 1998b). Also, *T. arizonensis* differs from the other *Trupanea* species previously studied, in that the meso- and metathorax are circumscribed by verruciform sensilla; whereas, only the mesothorax in *T. nigricornis* was circumscribed by verruciform sensilla (Goeden and Teerink 1997, 1998; Goeden et al. 1998a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998). *Trupanea arizonensis* differs from its symphagous congener in *Trixis californica*, *T. conjuncta*, in not being finely punctate nor barrel-shaped, and *T. arizonensis* also has

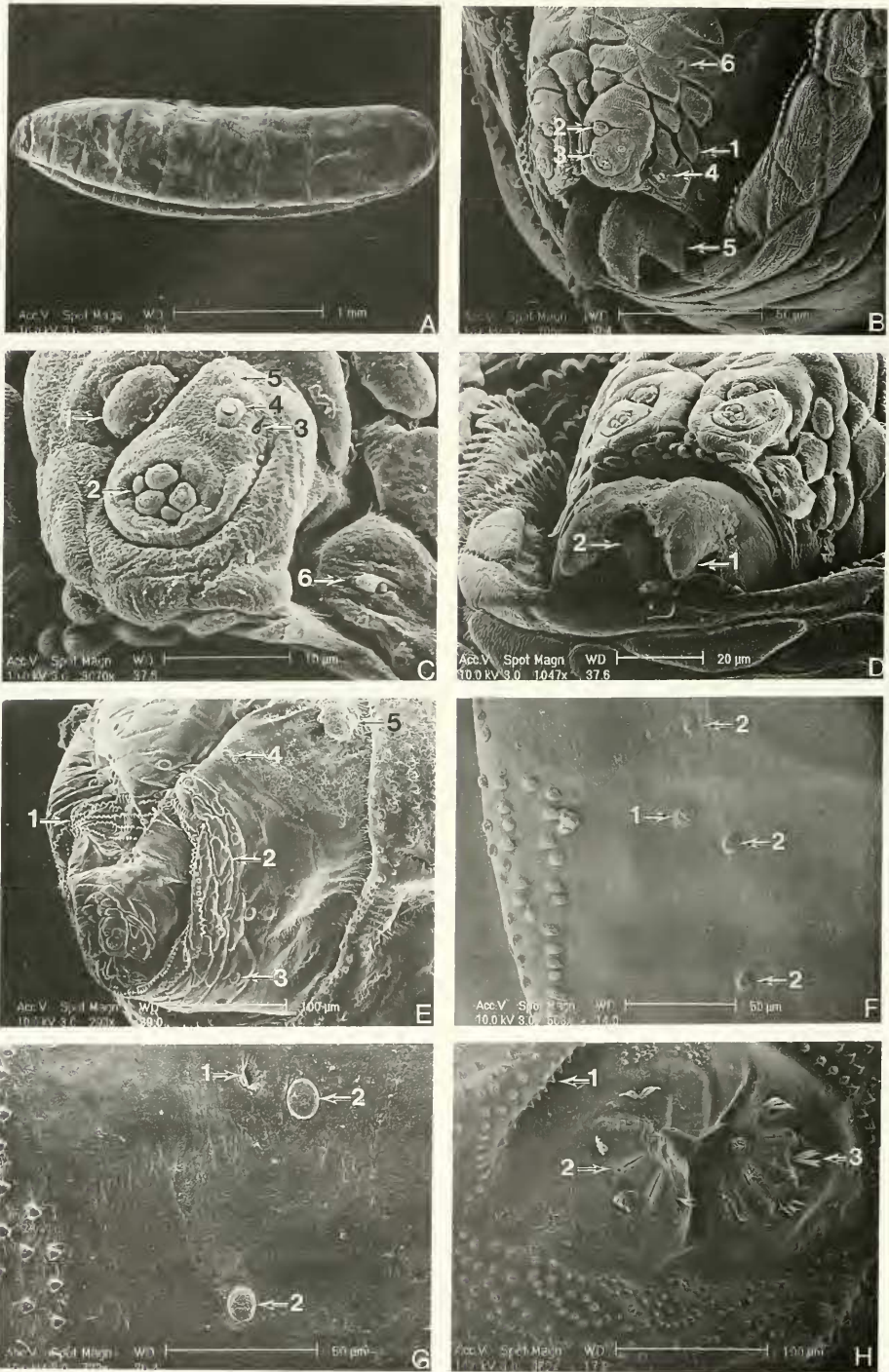


Fig. 3. Third instar of *Trupanea arizonensis*: (A) habitus, anterior end to left; (B) gnathocephalon, anterolateral view, 1, rugose pads, 2, dorsal sensory organ, 3, anterior sensory lobe, 4, stomal sense organ, 5, mouth hook, 6, pit sensillum; (C) anterior sensory lobe, 1, dorsal sensory organ, 2, terminal sensory organ, 3, pit sensory organ, 4, lateral sensory organ, 5, supralateral sensory organ, 6, stomal sense organ; (D) gnathocephalon, ventral view, 1, mouth hook, 2, median oral lobe; (E) gnathocephalon, prothorax, lateral view, 1, minute acanthae,

fewer papillae in the anterior thoracic spiracle (Teerink and Goeden 1998).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines, (Fig. 4A); anterior end bears the invagination scar (Fig. 4B-1), and anterior thoracic spiracles (Fig. 4B-2); caudal segment circumscribed by minute acanthae (Fig. 4C-1); posterior spiracular plates bear three ovoid rimae (Fig. 4C-2) and four interspiracular processes, each with 3–5 branches (Fig. 4C-3). Sixty-four puparia averaged 2.68 ± 0.02 (range, 2.28–3.24) mm in length; 0.92 ± 0.01 (range, 0.76–1.16) mm in width.

DISTRIBUTION AND HOSTS

The distribution of *T. arizonensis* mapped in North America north of Mexico by Foote et al. (1993) is confined to several, mostly U.S. southern border locations in Arizona, California, and Texas.

Goeden and Ricker (1989) reported *T. arizonensis* as *T. actinobola* from *Trixis californica*, and as mentioned above, Goeden (1992) corrected this misidentification and thus provided the first and sole host-plant record for *T. arizonensis*. This host-plant belongs to the subtribe Nassauviinae in the tribe Mutisieae of the Asteraceae (Hickman 1993, Bremer 1994); this tribe rarely occurs in North America (Bremer 1994), and is represented by only three species in California (Munz 1974), the second of which, *Acourtia microcephala* deCandolle, does not host *T. arizonensis* (Goeden and Headrick 1991). The third plant species is the rare, unsampled, xerophytic shrub, *Hecastocleis shockleyi* A. Gray (Hickman 1993, Bremer 1994). In comparison, *T. actinobola*, apparently is confined to three subtribes of the different tribe Astereae in California (Goeden and

Teerink 1998b). Accordingly, *T. arizonensis* may be either a true monophage (one host-plant species) on *Trixis californica*, which occurs as far east as Texas in North America north of Mexico (Hickman 1993), or a near-monophage (one host-plant genus) on one or more of the 50 other congeners in the southwestern United States, Central, and South America and West Indies (Bremer 1994). Like several other tephritid species that we have studied, e.g., *Trupanea conjuncta* (Goeden 1987), *T. pseudovicina* Hering (Goeden and Teerink 1998), and *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991), *Trupanea arizonensis* represents a native southern California tephritid closely associated with a native host-plant, which is primarily distributed in Mexico and southward, where these tephritids remain little known.

BIOLOGY

Egg.—In 38 closed, preblossom, immature flower heads, all 130 eggs were inserted pedicel-last between the tips of the phyllaries, perpendicular to the receptacle, and among or within the florets and pappus (Fig. 5A). The diameters of the receptacles of 32 of these flower heads containing eggs averaged 2.6 ± 0.1 (range, 1.3–3.7) mm, and the 38 infested heads contained an average of 3.4 ± 0.3 (range, 1–9) eggs oviposited, mostly singly, or side-by-side in pairs (Figs. 5A, B), but also in groups of up to five, by one or more females.

Larva.—Upon eclosion, first instars tunneled into a single floral tube or ovule of an immature floret (Fig. 5C). An average of 2.1 ± 0.2 (range, 1–4) first instars was found feeding within 22 closed, preblossom flower heads. The receptacles of these heads averaged 3.1 ± 0.2 (range, 2.2–4.6) mm in diameter with an average of 18 ± 2

←

2, rugose pads, 3, verruciform sensillum, 4, verruciform sensillum, 5, anterior thoracic spiracle; (F) metathorax, 1, spiracle, 2, verruciform sensilla; (G) fifth abdominal segment, 1, spiracle, 2, verruciform sensilla; (H) caudal segment, 1, minute acanthae, 2, rima, 3, interspiracular process.



Fig. 4. Puparium of *Trupanea arizonensis*: (A) habitus, anterior end to right; (B) anterior end, 1, invagination scar, 2, anterior thoracic spiracle; (C) caudal segment, 1, minute acanthae, 2, rima, 3, interspiracular process.

(range, 15–24) florets, of which an average of only 1.6 ± 0.2 (range, 1–3) florets, or 9% (range, 4–17%), were damaged. No receptacles within these 14 infested flower heads was pitted by first-instar feeding.

Second instars fed solitarily at the distal ends of individual ovules or soft achenes within different florets of separate preblossom and open flower heads, respectively. Their mouthparts were directed towards the receptacles. Receptacles of 16 flower heads containing second instars were not pitted and averaged 3.4 ± 0.2 (range, 2.3–4.8) mm in diameter. These flower heads contained an average of 1.6 ± 0.2 (range, 1–3) second instars that had damaged an average of 1.8 ± 0.2 (range, 1–4) ovules, or 11% (range, 6–22%) of an average total of 17 ± 0.8 (range, 12–20) ovules per flower head.

Most third instars also confined their feeding to the same single, separate ovule or soft achene at the centers, and less commonly at the margins, of preblossom or open flower heads (Fig. 5D). Third instars fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles, and on the distal parts of the ovules or soft achenes, well above the receptacles (Fig. 5D). In 28 flower heads averaging 4.0 ± 0.1 (range, 3.1–5.0) mm in diameter and containing an average of 1.5 ± 0.2 (range, 1–5) third instars, an average of 1.6 ± 0.2 (range, 1–5) ovules were damaged, or 9% (range, 4–25%). Thus, each larva confined its feeding to the distal parts of a single floret, at most including corolla tube and contents, pappus, and upper part of the ovule (Fig. 5D); the ovule continued to grow and functioned as a nutrient sink (Harris and Shorthouse 1996) augmented by the larva which fed mainly on sap drawn to the cuplike depression in the distal end of the ovule (Fig. 5D). This mode of feeding is the least damaging to host-plant reproduction, as well as the most exquisitely evolved manner of sap-feeding yet reported among florivorous Tephritidae (Headrick and Goeden 1998). This manner of larval feeding, first reported by Headrick and Goeden (1990b), apparently is facultative, undetected, or absent in some florivorous species, e.g., *Paracantha gentilis* Hering (Headrick and Goeden 1990a, b), *Trupanea nigricornis* and *T. bisetosa* (Knio et al.

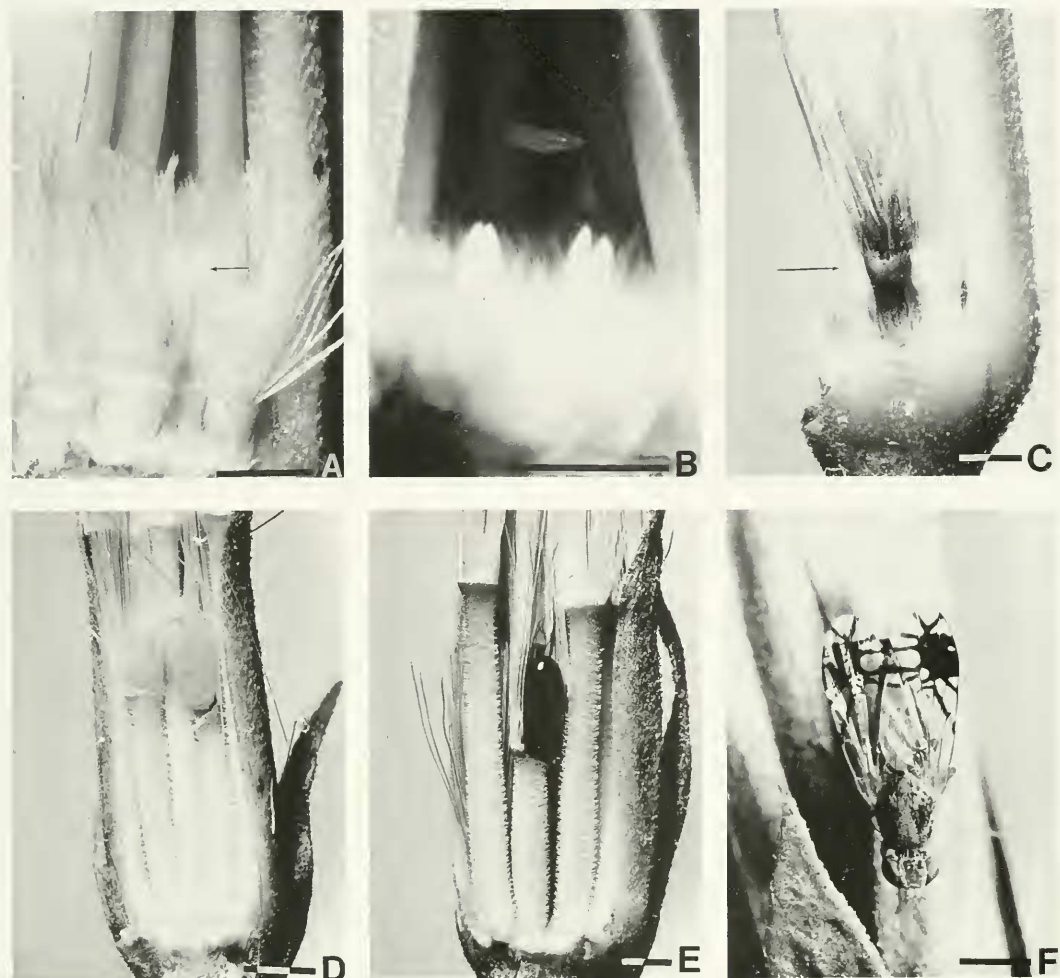


Fig. 5. Life stages of *Trupanea arizonensis* in or on *Trixis californica*: (A) one pair of eggs (arrow) inserted among immature florets in closed, preblossom flower head; (B) two pairs of eggs inserted among florets in closed, preblossom flower head; (C) first instar tunneling in single floret (arrow); (D) two third instars feeding on separate soft achenes; (E) single puparium atop stunted achene in flower head; (F) adult female at rest on flower head. Lines = 1 mm.

(1996b); although it also has been reported in some gallicolous species, e.g., *Aciurina thoracica* Curran (Headrick and Goeden 1993), and is facilitated by specialized mouthparts in larval Tephritinae (Headrick and Goeden 1990a, 1993, 1998).

Upon completing feeding, the larvae oriented their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 5E).

Pupa.—Flower heads containing puparia (Fig. 5E) contained the greatest amounts of damage produced by the seed-feeding lar-

vae of *T. arizonensis*. The receptacles of 41 open and postblossom flower heads containing puparia averaged 4.4 ± 0.1 (range, 2.9–6.2) mm in diameter and bore an average total of 19.2 ± 0.6 (12–26) soft achenes, of which an average of 2.2 ± 0.3 (range, 1–9) soft achenes or 13% (range, 4–58%) were damaged. Again, no receptacles were fed upon. These heads contained an average of 1.8 ± 0.2 (range, 1–7) puparia. Most puparia of *T. arizonensis* were found near the centers of the flower heads, and all had their anterior ends facing away from

the receptacles, and their long axes were perpendicular to the receptacles (Fig. 5E).

Adult.—Adults (Fig. 5F) emerged from mature, postblossom flower heads, and were long-lived under insectary conditions, as 15 unmated males lived an average of 89 ± 14 (range, 11–194) days, and six virgin females averaged 126 ± 7 (range, 110–150) days. Like several other, monophagous and nearly monophagous congeners studied (Goeden 1988, Goeden and Teerink 1997, 1998), the longevities of these flies were among the longer averages and maxima for adults that we have recorded for native species of nonfrugivorous Tephritidae from southern California. Such longevities are commensurate with the aggregative type of life cycle ascribed below to this tephritid. The pre-mating and mating behaviors of *T. arizonensis* were not studied in the field, and again, like most congeners that we have studied, adults would not mate in petri dish arenas otherwise so useful with many other, noncongeneric, nonfrugivorous species (Headrick and Goeden 1994).

Seasonal history.—The life cycle of *T. arizonensis* in southern California appears to follow an aggregative pattern in which the long-lived adults in reproductive diapause over-summer in riparian habitats and mountain meadows. They return to lower elevations in the fall, and following the onset of winter rainfall, aggregate on *Trixis californica* in the low-elevation Colorado Desert in winter (January–February) to mate and later to oviposit (March–April) (Headrick and Goeden 1994). A single annual generation is produced each year and most of the life span of *T. arizonensis* is spent as an adult.

Natural enemies.—*Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from individual puparia of *T. arizonensis* as a solitary, larval-pupal endoparasitoid; however, at least some of the other species of parasitoids reported from *Tomoplagia cressoni* Aczél (Goeden and Headrick 1991) and *Trupanea conjuncta* (Goeden 1987), which co-occur in symphagy in the heads

of *Trixis californica* (Goeden and Ricker 1989, Goeden 1997), probably also parasitize *T. arizonensis*.

ACKNOWLEDGMENTS

We thank Andrew C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, for identification of plants mentioned in this paper. The parasitoids were identified by Harry E. Andersen, Huntington Beach, California. We also are grateful to Kristine Gilbert for technical assistance, and to D. H. Headrick for his helpful comments on an earlier draft of this paper.

LITERATURE CITED

- Bremer, K. 1994. Asteraceae Cladistics & Classification. Timber Press, Inc. Portland, Oregon.
- Cavender, G. L. and R. D. Goeden. 1982. Life history of *Trupanea bisetosa* (Diptera: Tephritidae) on wild sunflower in southern California. *Annals of the Entomological Society of America* 75: 400–406.
- Foote, R. H. 1960. A revision of the genus *Trupanea* in America north of Mexico. United States Department of Agriculture Technical Bulletin 1214. 29 pp.
- Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. *Bulletin of the California Insect Survey* 7, 117 pp.
- Foote, R. H., F. L. Blanc, and A. L. Norrbom. 1993. Handbook of the Fruit Flies (Diptera: Tephritidae) of America North of Mexico. Cornell University Press, Ithaca, New York.
- Goeden, R. D. 1985. Host-plant relations of *Trupanea* spp. (Diptera: Tephritidae) in southern California. *Proceedings of the Entomological Society of Washington* 87: 564–571.
- . 1987. Life history of *Trupanea conjuncta* (Adams) on *Trixis californica* Kellogg in southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist* 63: 284–291.
- . 1988. Life history of *Trupanea imperfecta* (Coquillett) on *Bebbia juncea* (Bentham) Greene in the Colorado Desert of southern California (Diptera: Tephritidae). *Pan-Pacific Entomologist* 64: 345–351.
- . 1992. Analysis of known and new host records for *Trupanea* from California (Diptera: Tephritidae). *Proceedings of the Entomological Society of Washington* 94: 107–118.
- . 1997. Symphagy among florivorous fruit flies (Diptera: Tephritidae) in southern California, pp.

- 39–52 In Dettner, K., G. Bauer, and W. Vökl. eds., Vertical Food Web Interactions: Evolutionary Patterns and Driving Forces. Ecological Studies 130, Springer-Verlag, Heidelberg, Germany.
- Goeden, R. D. and D. H. Headrick. 1991. Notes on the biology, hosts, and immature stages of *Tomoplagia cressoni* (Aczél) in southern California (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 73: 549–558.
- Goeden, R. D. and D. W. Ricker. 1989. Phytophagous insect faunas of the desert shrubs, *Bebbia juncea* and *Trixis californica* in southern California. Annals of the Entomological Society of America 82: 325–321.
- Goeden, R. D. and J. A. Teerink. 1997. Life history and description of immature stages of *Trupanea signata* Foote (Diptera: Tephritidae) on *Gnaphalium luteo-album* L. in southern California. Proceedings of the Entomological Society of Washington 99: 748–755.
- . 1998. Life history and description of immature stages of *Trupanea pseudovicina* Hering (Diptera: Tephritidae) on *Porophyllum gracile* Benth (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 361–372.
- Goeden, R. D., J. A. Teerink, and D. H. Headrick. 1998a. Life history and description of immature stages of *Trupanea jonesi* Curran (Diptera: Tephritidae) on native Asteraceae in southern California. Proceedings of the Entomological Society of Washington 100: 126–140.
- . 1998b. Life history and description of immature stages of *Trupanea actinobola* (Loew) (Diptera: Tephritidae) on *Acamptopappus sphaerocephalus* (Harvey and Gray) Gray (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 100: 674–688.
- Harris, P. and J. D. Shorthouse. 1996. Effectiveness of gall inducers in weed biological control. Canadian Entomologist 128: 1021–1055.
- Headrick, D. H. and R. D. Goeden. 1990a. Description of the immature stages of *Paracantha gentilis* (Diptera: Tephritidae). Annals of the Entomological Society of America 83: 220–229.
- . 1990b. Resource utilization by larvae of *Paracantha gentilis* (Diptera: Tephritidae) in capitula of *Cirsium californicum* and *C. proteanum* (Asteraceae) in southern California. Proceedings of the Entomological Society of Washington 92: 512–520.
- . 1991. Life history of *Trupanea californica* Malloch (Diptera: Tephritidae) on *Gnaphalium* spp. in southern California. Proceedings of the Entomological Society of Washington 93: 559–570.
- . 1993. Life history and description of immature stages of *Aciurina thoracica* Curran (Diptera: Tephritidae) on *Baccharis sarothroides* Gray in southern California. Proceedings of the Entomological Society of Washington 95: 210–222.
- . 1994. Reproductive behavior of California fruit flies and the classification and evolution of Tephritidae (Diptera) mating systems. Studia Dipterologica 1(2): 194–252.
- . 1998. The biology of nonfrugivorous tephritid fruit flies. Annual Review of Entomology 43: 217–241.
- Hickman, J. C. (ed.) 1993. The Jepson Manual. University of California Press, Berkeley and Los Angeles.
- Knio, K. M., R. D. Goeden, and D. H. Headrick. 1996a. Descriptions of immature stages of *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) from southern California. Annals of the Entomological Society of America 89: 1–11.
- . 1996b. Comparative biologies of the cryptic, sympatric species, *Trupanea nigricornis* and *T. bisetosa* (Diptera: Tephritidae) in southern California. Annals of the Entomological Society of America 89: 252–260.
- Malloch, J. R. 1942. Notes on two genera of American flies of the family Trypetidae. Proceedings of the United States National Museum 92(3123): 1–20.
- Munz, P. A. 1974. A Flora of Southern California. University of California Press, Berkeley and Los Angeles.
- Teerink, J. A. and R. D. Goeden. 1998. Description of immature stages of *Trupanea conjuncta* Adams (Diptera: Tephritidae). Proceedings of the Entomological Society of Washington 100: 431–438.